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EMBRYOLOGICAL STUDIES ON THE NUCLEI AND
THEIR HOMOLOGIZATION IN THE VERTEBRATE
FOREBRAIN

BY

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LUND
C. W. K. GLEERUP

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I. Introduction

This paper is based on seven earlier papers on the ontogenesis of the vertebrate forebrain:

- I.* A contribution to the ontogenetic development of the nuclei in the forebrain in *Lepisosteus*. *Acta Anat.* 9, 297, 1950 a.
- II.* Contributions to the ontogeny of the everted forebrain. *Kungl. Fysiogr. Sällsk. Förhandl.* 20, nr 8, 1950 b.
- III.* Some remarks on the ontogeny of the telencephalon in some lower vertebrates. *Acta Anat.* 11, 537, 1951 a.
- IV.* On the ontogeny of the reptilian forebrain. Nuclear structures and ventricular sulci. *J. Comp. Neur.* 95, nr. 2, 1951 b.
- V.* Contributions to the knowledge of the medial wall of the reptilian forebrain. *Acta Anat.* 13, 90, 1951 c.
- VI.* The nuclear development in the mammalian forebrain with special regards to the subpallium. *Kungl. Fysiogr. Sällsk. Handl.* 61, nr. 9, 1951 d.
- VII.* Contributions to the ontogeny of the nuclear structures and the ventricular sulci in the vertebrate forebrain. *Kungl. Fysiogr. Sällsk. Handl.* 62, nr. 3, 1951 e.

In the text these papers will be referred to with the figures *I—VII*.

These papers discuss the following problems in some different vertebrates:

1. The development of the external and the ventricular form of the telencephalon (*II—IV*, *VI—VII*).
2. The earliest cell migration and the formation of the so-called "Grundgebieten" (chiefly *VII*).
3. The development of the nuclei from the "Grundgebieten" (*I*, *IV—VII*).
4. Some problems of homology (*I*, *III*, *VI*).

In this paper the results obtained in the papers *I—VII* will be assembled with observations previously described in the literature. The problems mentioned above will be discussed. Particular stress will be laid on the homologization of the nuclei of different vertebrates. The pallial formations and the bulbus olfactorius, however, will only be cursorily discussed. The subpallial nuclei will be especially emphasized.

II. The principles of the homologization of brain nuclei

As is apparent from the surveys of literature given earlier by the author (I—VII), many investigators have studied the adult and in some cases also the embryonal nuclei of the telencephalon in many different vertebrates. When the nuclei have been named, many authors have used neutral signs of a chiefly descriptive nature. Among later authors, who have used such names, the following may be noticed: CROSBY (1917), HERRICK (1922), ROSE (1923), WESTON (1937), MEADER (1939). Other investigators have used the same names in different species and supposed homologies between the nuclei, named in the same way. Only in a few cases have strictly defined principles been followed when the homologies have been settled. Usually they have been determined with the aid of combinations of the topographical position, the embryonal development, the fibre connexions, and the cytoarchitecture, with emphasis on one of these factors.

In earlier papers the greatest stress was laid on the topographical position of the nuclei, their cytoarchitecture and especially on the fibre connexions between the nuclei. This was done by KAPPERS (1906, 1907, 1908, 1928), JOHNSTON (1911 a and b, 1912 a and b, 1915) and SHELDON (1912). The ventricular furrows were often used as morphological marks of great importance, for instance in KUHLENBECK's works, which were summarized in 1929. In later papers by JOHNSTON (1916, 1923 a) the embryonal development of the nuclei was also taken under consideration, especially their relations to the ventricular furrows and ridges during ontogenesis.

HOLMGREN has studied the vertebrate forebrain in some papers (1919, 1920, 1922, 1925, 1946, HOLMGREN-VAN DER HORST 1925) and settled some homologies on a chiefly embryological basis. PALMGREN (1921) defined this comprehension, when studying the development of the mesencephalon and the metencephalon, in the following words: "If it can be proved that two nuclei are formed from the same position of a (secondary) segment, they are homologous." Embryological principles were also followed by SÖDERBERG (1922), BÄCKSTRÖM (1924), RENDAHL (1924), BERGQUIST (1932) and RUDEBECK (1945) on different problems in the comparative anatomy of the vertebrate forebrain. BERGQUIST tried to derive all nuclei in the region studied — the diencephalon of lower vertebrates — from so-called "Grundgebieten", i. e., the firstly visible aggregations of cells. The "Grundgebieten" were also looked upon as zones of growth, i. e., proliferation regions. All homologies were based on the topography of these regions.

HERRICK (1933 c) was opposed to BERGQUIST's opinion. He pointed out, that the ventricular furrows in the adult amphibian brain delimits regions, which are histological and functional unities, while BERGQUIST's "Grundgebieten" usually lie around the ventricular furrows. He emphasized, that COGHILL's (1928) investigations have shown that the indifferent cells differentiate to neuroblasts in zones, lying between the proliferation zones, i. e., between the ventricular furrows. He pointed out, that one must take into consideration both the indifferent proliferation zones and the differentiation zones, "but for practical purposes of descriptive anatomy

and experimental physiology, the differentiation, which looks forward to functional efficiency is vastly more significant, ..." (p. 245). HERRICK was of the opinion that too little attention had been paid to the fibre anatomy: "Nerve fibers are quite as important as cell bodies in cerebral organization and as elements in cerebral forms" (p. 243). A similar opinion was held by HERRICK in 1948.

HERRICK has made a very detailed analysis of the adult urodele forebrain (1927, 1933 a and b). The cell configurations and the fibre anatomy were described in detail, and with the results obtained as a basis the brain was subdivided into regions, which were looked upon as homologies of the mammalian nuclei. But he wrote: "In suggesting these comparisons it must be borne in mind that in the nature of the case such homologies cannot be exact". In some later papers (1937, 1938 a—c, 1939) some embryonal *Ambystoma* stages were described, also very closely. The structures previously described in the adult brain were followed during ontogenesis, and HERRICK tried to derive them from COGHILL's differentiation zones.

The term homology was firstly defined by OWEN (1843). He used it without relation to any phylogenetic relationship or ontogenetic similarity between the organs in question. He let the term express only a common structural plan in different species. This idea was carried to its logical extreme by NAEF (1927, 1931) and JACOBSHAGEN (1927), who both looked upon the conception of homology as a purely abstract idea. JACOBSHAGEN introduced the term "Bauplan", and wrote: "Organe, die in einem Bauplan oder dessen Grundformteilen denselben Bestandteil verkörpern, nennen wir, unbekümmert um etwaige Form- und Funktionsunterschiede, homolog." Within comparative neurology this conception was used for the first time by KUHLENBECK, who endeavoured to draw up a "Bauplan" for the telencephalon (1929 a) and for the diencephalon (1929 b). Among later authors, who have followed KUHLENBECK, GERLACH (1947) may be mentioned.

HAECKEL (1866) introduced DARWIN's evolution theory in the comparative anatomy and looked upon homologies as expressions for phylogenetic relationships. This point of view has been widely spread. But it is often impossible to study the phylogenetic development directly, and for this reason homologies have been based to a great extent on the ontogenetic development. Very soon, however, difficulties arose, when one tried to solve the problems of homologies in this way. SZARSKI (1949) summarized and discussed these difficulties, and came to the conclusion, in principle previously put forward by MOMENT (1945), that in addition to the phylogenetic meaning of the term there are two ontogenetic meanings. Two homologous organs develop either from the same anlage or from different anlages under similar influence.

When homologies in the central nervous system are studied, it is impossible in most cases to follow the phylogenetic development, but we are entirely referred to the ontogenetic development. As yet we know very little about the factors which influence the nerve cells in the formation of the brain nuclei during ontogeny,

so we cannot approach the developmental mechanistic meaning of the word homology. Evidently we must resort to a study of the course of the ontogeny of the nuclei in order to settle the homologies between the brain nuclei. If it can be proved, that two nuclei in different species develop from the same anlage and in a similar way, they must be looked upon as homologous. The longer the developments of two nuclei are similar, the stricter is the homology between the nuclei. It is probable, however, that the homologies reached in this way, must be supplemented with new ones, when the developmental mechanistic conditions are better known.

During ontogeny there are in principle three different processes in the wall of the nerve tube:

1. the cell proliferation in the ventricular layer
2. the cell migration and the grouping of the migrated cells
3. the cell differentiation from the indifferent ectoderm cell to the differentiated nerve or glia cell with their fibre connexions.

The cells which build up the brain nuclei are formed by the cell proliferation and the cell differentiation. The actual brain nuclei, however, develop by the migration of the cells and the grouping of the migrated cells into separate fields: nuclei. Only the last-mentioned process — the cell migration and the grouping of the migrated cells — thus take part in the formation of the nuclei. According to the author's opinion only these processes ought to be taken under consideration when the nuclei are to be homologized.

The cytoarchitecture and the fibre connexions of a nucleus depend on the cell differentiation processes which have taken place within the nucleus, and they mirror the function of the nucleus. As homologous nuclei and other homologous organs are often functional equals, they are frequently similar from a cyto-architectural point of view and with regard to the fibre connexions. But there has never been any demand for homologous organs to have similar functions. Neither can brain nuclei meet this requirement, as was pointed out by HOLMGREN (1922) et al. According to the present author's opinion a homology can therefore never be based exclusively on such studies. Only by following the ontogenesis of a nucleus, e. g. by studying the cell migration and the grouping of the migrated cells, can homologies be obtained.

It is possible that the development of the fibre connexions and other processes, possibly taking place in the wall of the nerve tube, influence the cell migration and the grouping of the migrated cells, but nothing as yet is known of this phenomenon. The results of this hypothetical influence are directly observed when the migration and the grouping of the cells are studied, but their nature cannot be unveiled in this manner. It is the author's intention to study directly these processes in subsequent papers and to try to settle their developmental mechanistic relations.

As the mutual topography of the different nuclei are naturally strongly influenced

by changes in the form of the telencephalon, the author has discussed this problem somewhat in the papers mentioned above. The ventricular relief has also been investigated, as many authors, e. g. KUHLENBECK, JOHNSTON, HERRICK et al., have laid great emphasis on the topographical relation between the nuclei and the ventricular furrows and ridges when homologizing the nuclei.

III. The telencephalic evagination processes

In all craniotes the foremost part of the nerve tube is the object of two large evagination processes on each side: the optic evagination and the hemispheric evagination. Besides these there are paired and unpaired evaginations in the roof, forming the paraphysis, epiphysis, saccus dorsalis etc.

The two first-mentioned evaginations represent two relatively fixed points in the forebrain morphology. They commence early — the optic evagination earlier than the hemispheric evagination.

The hemispheric evagination develops very dissimilarly in different vertebrate species. As has been pointed out previously (*III*) two sorts of evagination can be distinguished after its localization: true evagination, when only the nervous substance is included, and pseudoevagination, when the process is localized to the taenia telencephali and includes both the tela and the nervous part of the wall.

The earliest development of a lateral ventricle occurs in all species investigated by a laterally directed true evagination. In all of these species except *Petromyzon* this lateral evagination appears as an inversion process. Its strength varies greatly. In actinopterygians it is very small and soon disappears. It has here the appearance of an inversion sulcus (*II*, *III*). In anurans it is also little developed, but remains all through embryonal life. In elasmobranchs, on the contrary, it is very large.

From the hemispheres formed primarily by the lateral true evagination, rostral and caudal lobes develop in most species through a co-operation of true and pseudoevaginations.

In *Petromyzon* (*VII*) the lateral true evagination is relatively small, and also the rostral and caudal lobes, developed from it, are small. Only a true evagination occurs.

In actinopterygians (*II*, *III*) no caudal lobe develops. The rostral lobe is formed chiefly by a pseudoevagination, but in ganoids and bony ganoids also a true evagination takes part. In these animals the picture is complicated by the eversion, which appears late in the development.

In all other species investigated both rostral and caudal lobes develop. The rostral lobes are formed in elasmobranchs, *Protopterus* and in anurans exclusively by a true evagination. In batoidei the rostral lobes are very small. In urodeles, *Epiceratodus* and reptiles (except *Tropidonotus*) there is also a strong rostral pseudoevagination, forming a septum ependymale, while in mammals and *Tropidonotus* no or only a very slight rostral pseudoevagination occurs (*III*, *IV*, *VI*).

There are also dorsal and ventral evaginations present. Especially typical for the *Epiceratodus* brain is the enormous ventral true evagination (*III*). A plexus chorioideus is formed by a dorsal pseudoevagination except in elasmobranchs. In anurans this formation is small.

The caudal lobes are formed in elasmobranchs, urodeles, anurans and most reptiles by a caudal true evagination. In certain reptiles (*Chrysemys* i. a.) and in mammals there is also a caudal pseudoevagination present (*IV*, *VI*).

In some species (i. a. reptiles, *V*) the septum endymale is secondarily reduced. According to the author's opinion this takes place by an evagination of the endymal lamina into the plexus chorioideus formation. The author has, however, never found any signs of a transformation of the endymal septum to nervous substance, as BURR (1922) thought was the case in urodeles.

A secondary thinning of a nervous part has been observed by RUDEBECK (1945) and the author (*V*).

It is evident, that the telencephalon from this point of view exhibits very different qualities throughout the vertebrate series. It seems difficult to understand the phylogenetic relations between the different brain types. Some attempts have been made on this subject (i. a. HOLMGREN 1922, RUDEBECK 1945), but according to the author's opinion too little is known of the factors which cause the different modes of development, to permit any conclusions on their phylogenetic relationship.

The changes in the form, however, play a great rôle in the understanding of the topographical relations between the different brain nuclei, and it is from this point of view the author looks upon the problem of form development. The author will discuss this problem further in chapter 9 of this paper.

IV. The nature of the telencephalic ventricular sulci

As pointed out previously (*II*) the ventricular furrows were at first looked upon as limits between different regions of the brain, and great stress was laid on the furrows, when the nuclei were homologized. Among others HERRICK, JOHNSTON, and especially KUHLENBECK emphasized them greatly. As mentioned above, BERGQUIST showed that the diencephalic ventricular furrows were not situated between the different "Grundgebieten" in the brain wall, but usually within them. During the ontogenesis they may be dislocated towards the margins of the regions and become limiting furrows or disappear. BERGQUIST called these furrows "Proliferations-furchen". RUDEBECK described corresponding "proliferation furrows" in the dipnoan and amphibian telencephalon. The author (*II*) followed these authors when the ventricular contour of the actinopterygian forebrain was described. As pointed out then the proliferation furrows are rather inconstant phenomena. Their position, depth and length vary greatly in different stages and different species. BERGQUIST (1932, p. 73) was of the same opinion.

From the studies on the mitotic distribution made by BERGQUIST, RUDEBECK and

the author (*II*), it is apparent, that the mitoses are crowded around some of the ventricular furrows. It seems as if the proliferation causes the furrows. This process can possibly occur in the following manner: the cells, formed by the proliferation are pushed up in banks on each side of the centre of the proliferation and form in this way a furrow. If this hypothesis is correct, a more vivid proliferation ought to lie around a deeper furrow. If the proliferation is strongest sometimes in one part of the ventricular wall, sometimes in another, the furrow moves to and fro. According to this hypothesis the furrows are signs of regions with vivid proliferation and their shifting and variations in depth mirror changes in the proliferation intensity.

This hypothesis is supported by some observations on the mitotic distribution, but other more exact methods are necessary if it is to be accepted or rejected. In this paper the hypothesis sketched above will be accepted as a working hypothesis. The author intends to return, if possible, to this problem on another occasion.

When the strength of the proliferation during the later part of the ontogenesis diminishes, these furrows ought to disappear, too. But by the proliferation new cell masses have been formed, which form thickenings within each regio. In this way new furrows, boundary furrows, appear between the areas.

According to this opinion the boundary furrows will not develop from the proliferation furrows. The observations actually made on relations between the boundary furrows and the proliferation furrows (BERGQUIST, RUDEBECK, the author *II*) may be explained with the hypothesis, put forward above: if a proliferation furrow shifts over a regio in a certain direction during ontogenesis, it will appear to be the forerunner of the boundary furrow in the same direction. A fact, which supports this hypothesis is that the same proliferation furrow in different species can "develop" to different boundary furrows (BERGQUIST, RUDEBECK, the author *II*). The sulcus subpallialis dorsalis shifts in *Protopterus* dorsalward and forms the sulcus limitans pallii lateralis, while in anurans and actinopterygians it forms the sulcus limitans lateralis (cf. table 6, paper *II*).

No observations have been made on any relation between the cell migration and the ventricular furrows. As pointed out above, the cell migration and not the cell proliferation must be taken under consideration when the nuclei are homologized. Only if the proliferation regions are identical with the migration regions, are the ventricular furrows of any importance for the questions studied in this paper. This problem will be further discussed in the next chapter. — The author has also made some observations, which show that it is unsuitable to use the furrows as a basis for a homology (*VI*).

HERRICK (1938 c) was of quite another opinion: "the morphological value of the ventricular sulci is beyond question. These very conservative features furnish our best guides for the analysis of cerebral structure and its transformations". But he emphasized that one must be rather cautious when drawing conclusions with the aid of them.

V. The earliest cell migration

BERGQUIST (1932) derived the diencephalic nuclei in lower vertebrates from areas in the ventricular gray, "Grundgebieten". By counting the mitoses he showed that these regions are proliferation centres.

RUDEBECK (1945) distinguished corresponding structures, so-called proliferation regions, in the forebrain of dipnoans. In younger stages they represent accumulations of mitoses. In later stages they represent morphological subdivisions of the cell crowds.

The author has studied the earliest cell migration in the telencephalon of some different vertebrates (*IV*, *VI*, *VII*). Summarized it can be described in the following way:

In very early stages the cell material of the brain is made up of undifferentiated cells, which form a stratum matricis.¹ This is differentiated into a stratum ependymale¹ and a stratum cellulare¹. The latter can retain its ventricular position or cells can migrate and form one or more peripheral layers (migrated layers; proliferation layers). PALMGREN (1921) and BERGQUIST distinguished a stratum cellulare externum (= the peripheral layer) and a stratum cellulare internum (= the ventricular layer). In some species no distinct peripheral layer develops. The cells migrate, but the cell crowd maintains its connexion with the ventricular gray. This is the case in the subpallium in *Petromyzon*, in the unevaginated part of the actinopterygian forebrain and in urodeles. In elasmobranchs, in the evaginated parts of the actinopterygian forebrain, in anurans and in amniotes the cells migrate and form a peripheral layer.

As is visible in the figure 1, no distinct limit can be drawn between these different sorts of migration, and all types must be looked upon in principle as the same process. This opinion is also supported by the fact, that both processes can take place in the rostral and the caudal parts of the same area in actinopterygians i. a.

Another fact is that within the same area successive proliferations and migrations can occur. This has been described especially in higher vertebrates, but also in some lower vertebrates. In some parts of the brain four successive proliferations have been described (*IV*). It seems probable that different forces cause the different proliferations to take place.

Because of these facts the author has rejected the names used by PALMGREN and BERGQUIST and has marked the layers proliferated and migrated successively with the indices I, II ...

The author will use the name of migration area for the ventricular areas, which correspond to the regions within which the first migration takes place, as described

¹ These names and the definitions on the conceptions of area and regio, used in this and a previous paper (*VII*), have been settled by the author after having conferred with Dr. BERGQUIST.

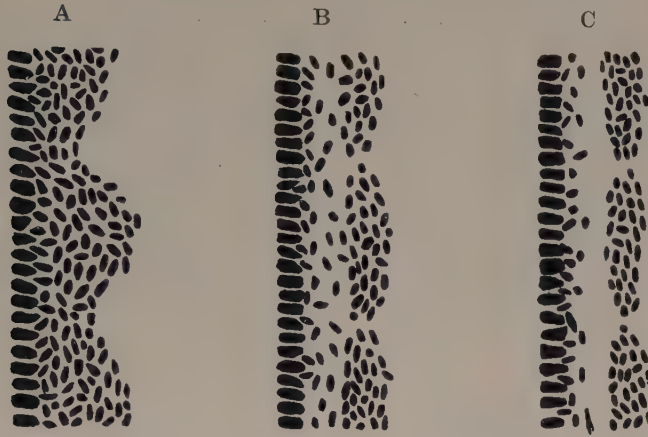


Fig. 1. Schematic drawings illustrating the transition (B) between a stage with ventriculally crowded cells (A) and a stage with a developed peripheral layer (C). The figures represent transversal sections through a regio, with the stratum ependymale situated to the left.

above. The latter thus represent the first signs of nuclear differentiation. In contrast to these the author will put the proliferation area, corresponding to the centres of proliferation, which with the methods of observation now available, represent aggregations of mitoses. According to BERGQUIST's, RUDEBECK's and the present author's (II) previous opinion, these two formations are identical, so that every migration area represents a proliferation area.

Within each migration area a proliferation must take place, and an aggregation of mitoses must be present. Besides the pattern of mitoses, formed in this way, there must be other patterns present, caused by the changes of the form of the brain wall, i. a., the optic and hemispheric evaginations. It seems to be impossible to determine whether a mitosis belongs to a mitotic pattern of one sort or another. If only the mitotic pattern that corresponds to the migration areas is developed, as is probably the case in the actinopterygian telencephalon and in the diencephalon of most species, the migration areas can probably be identified in this way at earlier stages than those, where the areas can be directly observed. Generally the form developmental processes and the development of the migration areas are simultaneous. In these cases it is impossible to say, where a migration area is developing only by studying the mitotic pattern. As has been emphasized above, it is the migration of the cells and the development of the migration areas that are of interest, when the problems, discussed in this paper, are to be solved. For this reason the mitotic patterns will not here be taken under consideration.

The first visible signs of nuclear differentiation, e. g., the migration areas, will then be used as the only basis for the homologies, proposed by the author.

VI. The homologization of the migration areas

If the migration areas are to be used for homologizing the nuclei developed from them, the migration areas of different species must at first be homologized with one another. In the paper *VII* their position and appearance in representatives of different vertebrate classes have been described. In broad outlines two migration areas have been distinguished in all species, a dorsal one and a ventral one. The relation between these areas and the diencephalic areas, as described by BERGQUIST, have been studied. Somewhat dissimilar conditions were shown to exist in different vertebrates.

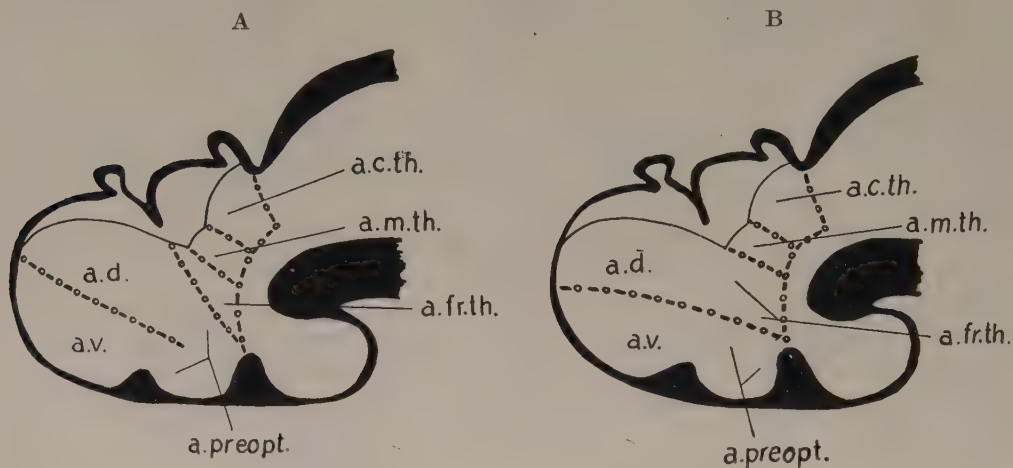


Fig. 2. Schematic drawings showing the topography of the migration areas in elasmobranchs (A) and in other vertebrates (B). The drawings show the brains in medial view. The median section surface is black. The limits between the areas are marked with o-o-o-o.

In *Petromyzon*, actinopterygians, anurans, reptiles and mammals the area dorsalis telencephali continues without any limit in young stages into the area frontalis thalami. Not until later in the development is a limit between these two areas formed by the development of the structures typical of each part. In some cases an intermediate part is formed, which will be discussed in detail below. The area ventralis telencephali occupies the rostroventral part of the telencephalon with its caudal limit at the optic chiasma. Thus the area preoptica is a part of the area ventralis telencephali in these brains.

In elasmobranchs the area dorsalis telencephali is separated from the area frontalis thalami even in the youngest stages where a cell migration is visible. Caudally the area dorsalis and the area ventralis telencephali fuse and form an area preoptica.

A curious intermediate form between these two types is the urodele brain (*Ambystoma*). In the youngest stages, where a migration has just commenced, the

topography corresponds to that found in elasmobranchs. In later stages they are arranged as in other vertebrates. In an intermediate stage the limits are indistinct in the di-telencephalic transition zone.

These two types of arrangement of the migration areas are schematically shown in the figure 2.

In spite of these dissimilarities in the topographical relations between the migration areas in different vertebrates a homology between the area dorsalis telencephali of elasmobranchs and the area dorsalis telencephali of other vertebrates seems to be likely. They have the same position in the nerve tube, even if their caudal limits are somewhat different. In the same way a homology between the area ventralis telencephali of different species can be supposed. The difficulties arise when the transitory zones between these migration areas and the diencephalic ones are studied, e. g., the area preoptica and the structures situated dorsal to it.

VII. The di-telencephalic boundary

The question of the di-telencephalic boundary has always been combined with the question of the segmentation of the nerve tube. It has long been known that there are bulges present in the nerve tube during the early morphogenesis. Very diverging opinions have been advanced, however, in the literature on their nature and significance. They are usually called segments or neuromeres, a term first introduced by ORR (1887). No agreement has been present with regard to the numbers and the position of the neuromeres in the prechordal part of the brain, the archencephalon. In RENDAHL's (1924) paper a detailed survey of the literature on this question is given.

Most authors have looked upon the telencephalon as the foremost segment or as the foremost part of an unsegmented prosencephalon (NEAL 1898). WEBER (1900), however, was of the opinion that the telencephalon includes two segments.

From this point of view the di-telencephalic boundary has been regarded as the boundary between the first and the second neuromere or segment, i. e., a strictly defined morphological limit. VON KUPFFER (1906) tried to solve the difficulties in determining the ventricular position of this boundary by identifying it with the sulcus intraencephalicus anterior.

JOHNSTON (1909) looked upon the telencephalon as "a complete segment or ring of the brain as His believed" (p. 532). The ventricular boundary was defined in the following way: "The telencephalon is bounded behind in young embryos by the optic vesicles and the primitive optic groove, in adults by the velum transversum and the recessus preopticus; in mammals by a line or plane passing immediately behind the interventricular foramina and the chiasma ridge" (p. 532).

RUDEBECK (1945) was of the opinion that the telencephalon in dipnoans and amphibians develops from the two rostralmost proliferation zones, while the diencephalon is formed by the zones following caudal to them. According to his

and BERGQUIST's (1932) opinion the proliferation zones form transversal bands in the nerve tube.

A division, which was completely based on cytoarchitectural conditions, was made by HEIER (1948) in *Petromyzon* between the diencephalon and the telencephalon on the ventricular surface. The limit was drawn through the commissura superior, caudal to the "primordium hippocampi" (= the eminentia thalami of HOLMGREN a. o.), the corpus striatum and the nucleus preopticus down to the optic chiasma. He could not decide if it runs rostral to, through, or caudal to the chiasma ridge. He thought it probable that it passes through the rostral part of the commissura postoptica.

Contrary to these authors, DART (1925) wrote, that the division into a telencephalon and a diencephalon is "an artificial division". He based his opinion chiefly on the functional relations of the regions in question.

In a paper not yet published, BERGQUIST (1951) makes a detailed analysis of the bulges from the nervous system of the brains of some different vertebrates. These bulges, the neuromeres, are externally separated by furrows, fissurae interneuromericae, while the ventricular depression in each neuromere is called sinuatio neuromerica. BERGQUIST, however, does not look upon these neuromeres as complete segments. He also describes a certain variation of the neuromeres in the foremost part of the nerve tube.

The apprehension of the telencephalon as a complete segment is definitely contradicted by the investigations made by SCHULTE-TILNEY (1914), KINGSBURY (1920, 1922), BURR (1922) and JOHNSTON (1923 b). These authors have all tried to identify the rostral limits of the four parts of the nerve tube, described by HIS (1888): the floor plate, the basal plate, the alar plate and the roof plate. According to HIS' opinion the floor plate runs rostralward to the recessus infundibularis while the sulcus limitans (= the limit between the basal plate and the alar plate) ends in the recessus preopticus. JOHNSTON (1909) thought that the floor plate extended to the chiasma ridge and that the sulcus limitans ends in the recessus preopticus. According to SCHULTE-TILNEY (1914) the recessus mamillaris is the rostral limit of the floor plate. KINGSBURY (1920, 1922) showed the structural difference between the floor plate and the basal plate and fixed the rostral limit of the floor plate to the fovea isthmi. BURR (1922) and JOHNSTON (1923 b) agreed with KINGSBURY's opinion, but JOHNSTON drew the limit slightly more rostrally than KINGSBURY did. The sulcus limitans ends in the recessus mamillaris according to KINGSBURY, and JOHNSTON (1923 b) agreed with this. BURR thought that the recessus opticus was the rostral end-point of this furrow, and HEIER (1948) was of the opinion that it ended in the foramen Monroi. He made, however, no embryological investigations.

Thus there is no part of the floor plate in the telencephalic "segment". The basal plate does not enter this brain part, if the sulcus limitans ends in the recessus mamillaris or the recessus preopticus.

Even if the different bulges from the rostral part of the nerve tube are not complete rings or segments, they may have a certain morphological importance.

A certain variation is present in the vertebrate series, however, which throws doubt upon the importance of these structures.

BERGQUIST's (1951) *sinuatio neuromerica III* seems to be relatively constant. It always runs from the vicinity of the epiphysis anlage down into the hypothalamic anlage.

The *sinuatio neuromerica II* develops in relation to the optic evagination, and the *sinuatio neuromerica I* is identical with the hemispheric evagination.

In *Petromyzon* the *sinuatio neuromerica I* lies rostral to the *sinuatio neuromerica II* in the 7.5 mm stage (*hem.evag.* and *opt.gr.* resp., fig. 2, VII), and is separated from it by a di-telencephalic ridge, which is externally corresponded by a di-telencephalic groove (= *fissura interneuromerica I*, BERGQUIST 1951). In later stages the *sinuatio neuromerica II* diminishes.

Similar conditions are present in the 7.5 mm *Torpedo* stage (fig. 11, VII). In later stages the *sinuatio neuromerica II* fuses with a bulge situated caudal to the velum transversum. The latter has no correspondence in *Petromyzon*, as the velum transversum is here very faintly developed.

In a 4 mm *Rana* stage (fig. 39, VII) the *sinuatio neuromerica II* is short and fuses caudally with the *sinuatio neuromerica III*. Similar conditions are present in the 5 mm *Petromyzon* stage. In the 5.0 mm *Rana* stage (fig. 40, VII) the *sinuatio neuromerica II* lies free and has the same appearance as the *sinuatio neuromerica II* in the 7.5 mm *Petromyzon* stage. In the 6 mm *Rana* stage (fig. 41, VII) there is an inversion in its dorsal end, which here runs a little rostralwards. The inversion is the first sign of a hemispheric evagination (*III*), and thus corresponds to the *sinuatio neuromerica I* in *Petromyzon*, elasmobranchs etc. In *Rana* the *sinuatio neuromerica I* and *II* are fused. Caudal to them follows a ridge, the di-telencephalic ridge, which externally corresponds to the di-telencephalic furrow. In principle the same conditions are present in urodeles, dipnoans, reptiles and certain actinopterygians.

In mammals there is in early stages a hemispheric evagination and an optic evagination, separated by a ridge. In somewhat later stages they fuse. The conditions remind one of those in elasmobranchs.

It is apparent that difficulties are encountered when co-ordinating the observations on the rostral brain bulges in different vertebrates. BERGQUIST (1951) has also pointed out this. The present author is of the opinion that they are no fixed morphological formations but that the two rostralmost neuromeres are influenced by the hemispheric evagination and the optic evagination.

The groove described by VON KUPFFER in *Petromyzon* and elasmobranchs as the sulcus intraencephalicus anterior seems to be identical with my optic groove (cf. VII), e. g., the *sinuatio neuromerica II* (BERGQUIST). The same furrow in urodeles, anurans, dipnoans (RUDEBECK) and *Acipenser*, *Amia* (*II*) and reptiles (*IV*) is the fused hemispheric and optic groove (= the fused *sinuatio neuromerica I* and *II*). In *Lepisosteus* and *Cyprinus* no distinct optic groove is developed and the hemispheric groove here forms the groove previously named the sulcus intraencephalicus

anterior (II). In mammals the sulcus intraencephalicus anterior has been described (VI) as a connexion between the hemispheric evagination and the optic evagination. Caudal to it follows the optic groove.

A much clearer picture of the relations in the vertebrate forebrain during ontogenesis is given by the following argumentation according to the author's opinion: The hypothalamic anlage develops by the "Kopfbeuge". In connexion with this process a furrow or a bulge, running dorsoventrally, is formed, the sinuatio neuromerica III (BERGQUIST). Rostral to it two evagination processes take place: the hemispheric evagination and the optic evagination. In connexion with them two furrows develop: the hemispheric groove and the optic groove. These three furrows: the hemispheric groove, the optic groove and the sinuatio neuromerica III, can be connected in different ways. Caudally the hemispheric evagination is externally bounded by the di-telencephalic groove, BERGQUIST's fissura interneuromerica I. It runs ventralwards from the velum transversum, which forms its dorsalmost and deepest part. The ventral course of the di-telencephalic groove depends on how the hemispheric evagination and the optic evagination are developed in relation to each other. Usually the furrow runs down rostral to the optic stalk, but i. a. in the 7.5 mm *Torpedo* stage it runs down caudal to it. Thus it cannot reasonably be used as a boundary, because the position of such an early and constant structure as the optic vesicle can vary in relation to it.

According to this discussion the rostral part of the nerve tube is not divided into definite segments. A boundary between the telencephalon and the diencephalon, valid for all vertebrates, is therefore impossible to make from this point of view.

RUDEBECK was of the opinion that the telencephalon develops from the two rostralmost proliferation zones and the diencephalon from the following ones. According to him the dorsal part of the caudal telencephalic proliferation zone forms the pallium, while the ventral part of it gives rise to the area preoptica. Without doubt some of the cells, proliferated dorsally, build up part of the pallial area (= the area dorsalis telencephali), while cells, proliferated ventrally, partly enter the preoptic region. According to the author's opinion, however, the mitotic pattern described by RUDEBECK, is formed by the development of the hemispheric evagination dorsally and the optic evagination ventrally. Both these processes must be combined with a vivid proliferation, which causes the aggregation of the mitoses. It is not very surprising that they are fused into a band, as the two evagination processes in these animals are connected with a deep furrow, the sulcus intraencephalicus anterior. In this way the boundary proposed by RUDEBECK, can also be carried back to the hemispheric evagination and the optic evagination, as was the case with the segmentation in this part of the brain.

The conditions described in the last chapter, that the migration areas extend uninterruptedly between the telencephalon and the diencephalon in most species, also speaks against the existence of a morphological boundary between these parts of the brain.

VIII. The entrance of the olfactory nerve in the telencephalon

As described previously (VII) the olfactory nerve usually enters the telencephalon at the limit between the area dorsalis and the area ventralis telencephali. The only exceptions from this rule are actinopterygians, where somewhat divergent conditions are present in different species (VII). Around the entrance of the nerve a cellular area develops, which represents the anlage of the olfactory bulb.

In various species the nerve enters very differently far rostrally. In *Petromyzon* the entrance lies in the rostral end of the limit in question, but in *Torpedo* far caudally. In *Squalus* it enters far rostrally from the very beginning, but shifts caudalwards during the development. This shifting of course only means a stronger growth rostral to the nerve than caudal to it.

Another rostrocaudal dislocation is caused by the rostral evagination in most species.

RUDEBECK (1945) described another sort of shifting. According to this investigator the nerve first enters the dipnoan forebrain within the subpallium (= the area ventralis telencephali) but then shifts to the limit between the subpallium and the pallium (= the area dorsalis telencephali). The present author has had no dipnoan material suitable for these studies. RUDEBECK described the same process in amphibians, but the author has shown (VII) that the nerve here from the very beginning enters at the limit between the migration areas. RUDEBECK's statement is probably due to the fact that he has determined the boundaries of the areas in the stages in question with the aid of the mitotic pattern.

After BURR's (1916) investigations we know that the olfactory organ influences the development of the telencephalon in urodeles. BURR (1922) suggested that the ingrowth of the olfactory fibres into the telencephalon also causes the differentiation of cells and the grouping of them into nuclei. On urodeles he says, however: "While the presence of these fibers was undoubtedly the primitive stimulus of growth, the pattern of development has become so firmly fixed that the absence of olfactory fibers does not preclude differentiation" (p. 287). The relations between the ingrowing olfactory fascicles and the cell proliferation and the cell migration is certainly very complex. Against the theory that the ingrowing fibres should directly cause the development of the cellular areas is the fact that in many species, as *Petromyzon*, *Acipenser*, *Cyprinus* and amniotes, the areas develop much earlier than the nerve enters. In other species, as elasmobranchs and *Lepisosteus*, the nerve enters first and after some time the areas begin to develop. In amphibians finally, the entrance of the nerve and the differentiation of the areas are approximately simultaneous.²

² PIATT showed in a paper (An experimental approach to the problem of pallial differentiation, J. Comp. Neur. 94, 105, 1951) which the author did not receive until this paper was gone in press, that in the urodelian primordium hippocampi the cells migrated into cortical formations, even if the fibre fascicles, related to this part, were destroyed. This also argues in favour to the opinion, expressed above.

IX. The later differentiation of the telencephalic nuclei and their homologization

It is impossible to give a complete account here of all nomenclatures used on different nuclei in the vertebrate forebrain and for all proposals of homologies between them, previously made. Many of them are summarized in KAPPERS-HUBER-CROSBY'S (1936) work.

A. The pallial-subpallial boundary

Great confusion prevails already in drawing the boundary between the pallium and the subpallium. HOLMGREN (1922) defined these conceptions in the following way: "All parts dorsal to the zonae limitantes belong to the pallium, the parts ventral thereto are subpallial." In his work (1910) HERRICK gave a similar definition, but used two furrows, the fissura endorhinalis and the fissura limitans hippocampi as the lateral and the medial boundary resp. KAPPERS (i. a. in KAPPERS-HUBER-CROSBY 1936) gave a similar definition, but great stress was here laid on the fibre connexions of the regions in question. Also other authors distinguished between the pallium and the subpallium according to similar principles.

HERRICK (1933 c) on the contrary wrote: "Various attempts have been made by morphologists to formulate a structural concept of pallium — — —. All of these attempts (including my own of 1910) have failed because the pallium is not a primary morphological constituent of the vertebrate brain, but a secondary differentiation which gradually emerged within tissue of subpallial type" (p. 252). HERRICK introduced a physiological definition: "We may, accordingly, speak of a pallial part of the hemisphere only where there is present a complex system of associations more or less clearly separated in space from the primitive reflex pathway of the 'basal' or 'stem' portion of the hemisphere. Where this separation is incomplete we may speak of pallial primordia" (p. 255).

HOLMGREN (1925) showed, that the pallial structures of the reptilian forebrain developed from the dorsal part of the migrated cell layer in young stages, while the subpallial nuclei developed from the ventral part of this layer. The author has shown (IV, VI, VII) that in all vertebrates studied a similar derivation can be made. In all species investigated (*Petromyzon*, *Squalus*, *Torpedo*, *Acipenser*, *Amia*, *Lepisosteus*, *Cyprinus*, *Ambystoma*, *Rana*, *Phyllomedusa*, *Epiceratodus*, *Protopterus*, *Chrysemys*, *Alligator*, *Tropidonotus*, *Lacerta*, *Chamaeleon*, *Homo* and some other mammals) there is in early stages a division of the migrated cells into a dorsal region and a ventral region, the area dorsalis telencephali and the area ventralis telencephali respectively. The structures in *Homo*, long called pallial, develop from the area dorsalis. The author will, therefore, formulate the definitions of the pallium and the subpallium in the following way:

Pallium develops from the dorsal migration area of the telencephalon, subpallium from the ventral migration area.

With these definitions conceptions are settled that agree very well with the prevalent ones, especially with those used by HOLMGREN and his co-workers, even if some differences are present in some cases (urodeles, VII).

The conceptions defined in this way are purely morphological and are not directly related to the functional conceptions, defined by HERRICK. It seems to the author that a development occurs within the morphological pallial region in the vertebrate series towards the functional pallial conception, defined by HERRICK.

B. The pallium

The further development of this part will not be discussed in detail here. We know from HOLMGREN's (1922), SÖDERBERG's (1922), BÄCKSTRÖM's (1924) and RUDEBECK's (1945) papers that also in lower vertebrates (elasmobranchs, amphibians, dipnoans) cortical formations are formed during ontogenesis. They have been compared with the cortici of the amniote forebrain. The author (I, III) has shown that a similar division occurs in the evaginated part of the forebrain of ganoids and bony ganoids. According to the author's opinion (III) the division into three parts in the pallium in the unevaginated part of the forebrain of these fishes and the whole of the teleostean forebrain does not correspond to the amniote cortical formations, as HOLMGREN (1922) supposed.

Above it has been emphasized (chapter 6) that the pallium in early stages forms a unity with the area frontalis thalami in most species. The two regions can be separated later on in the ontogeny when the structures typical of each part develop. An intermediate part, however, is often left. In *Petromyzon* it forms an unevaginated lobus subhippocampalis (HERRICK-OBENCHAIN 1913 et al.), which has been included in the telencephalon by many authors (JOHNSTON 1912 a, HERRICK-OBENCHAIN, HEIER 1948) and in the diencephalon by others (HOLMGREN 1922, BERGQUIST 1932). Which of these conceptions one embraces is in the present author's opinion quite arbitrary, as the di-telencephalic boundary is not a fixed boundary (chapter 7).

In amphibians a massa cellularis reuniens (RÖTHIG 1923) and in dipnoans a nucleus preopticus pars superior (RUDEBECK) have been described. The amphibian massa cellularis reuniens develops just at the transition between the pallium and the area frontalis thalami (VII). RUDEBECK looked upon the dipnoan nucleus preopticus pars superior as the homologue of the amphibian massa cellularis reuniens, and said it was situated between the pallium and the area frontalis thalami.

Thus it seems as if the lobus subhippocampalis in *Petromyzon*, the massa cellularis reuniens in amphibians and the nucleus preopticus pars superior in dipnoans should be homologous. In amniotes the pallium is separated from the area frontalis thalami depending on the powerful development of the caudal lobe. In elasmobranchs the two areas are separated from the very beginning of their development.

In actinopterygians a cell column is situated in the caudal part of the telencephalon, the nucleus entopeduncularis or the nucleus taeniae. It was assumed

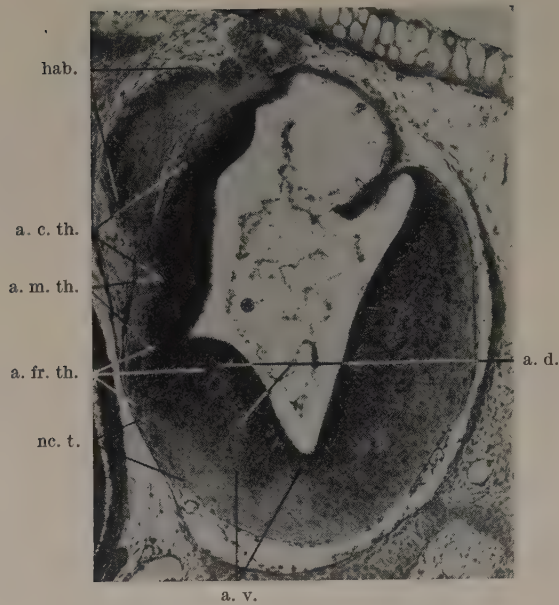


Fig. 3. Transversal section through the forebrain of *Lepisosteus*, the 14.5 mm stage, on a level with the caudal part of the commissure bed. The section shows the anlage of the nucleus taeniae from the transition between the area dorsalis telencephali and the area frontalis thalami. Staining: haematoxylin-eosin. 100 $\times$.

by HOLMGREN (1922) to be homologous with the nucleus taeniae in elasmobranchs and amphibians. But the nucleus taeniae develops in these animals from the caudal part of the tuberculum olfactorium, i. e., it is a subpallial nucleus. As was shown by BERGQUIST (1932) and confirmed by the author (*I*) the nucleus taeniae in actinopterygians develops from the area frontalis thalami and the dorsal part of the ventricular gray of the preoptic recess. In the section shown by the author (*I*) from a *Lepisosteus* embryo where this nucleus is developing, the transition between the pallial structure and the structure of the area frontalis thalami is visible. Just at the junction a cell plug extrudes. Later on it develops to the nucleus taeniae. For the sake of clearness the section in question is again reproduced here (fig. 3), with the different structures marked in detail. Thus the nucleus taeniae in actinopterygians holds the same morphological position as the structures discussed above in *Petromyzon*, amphibians and dipnoans, and they must be looked upon as homologous, even if their further development proceeds after different lines.

Finally a few words will be said on a structure, described in the reptilian brain under the name of hypopallium or the dorsal ventricular ridge. As JOHNSTON (1916), HOLMGREN (1925) et al. have shown, this structure develops in turtles from the ventral part of the pallium. It has also been shown in other reptiles (*IV*), that the corresponding structures (the neostriatum and the archistriatum KAPPERS) develop from the ventral part of the pallium. In mammals the claustrum develops from the

same place but in another manner. DE VRIES (1910 et al.), and HOLMGREN (1925) looked upon them as homologous. The author will not yet accept this homology, as too many differences in the anlage and development are present (VI). DART (1920) et al. have tried to identify the hypopallium in selachians and dipnoans but the nuclei in question have been shown by HOLMGREN (1922), BÄCKSTRÖM (1924) and RUDEBECK (1945) to be of a subpallial nature. The author has found no signs of a hypopallium in animals below reptiles.

C. The subpallium

a. Literature

Many attempts have been made to homologize the subpallial nuclei of different vertebrates. Especially the corpus striatum complex has given rise to many difficulties.

The analysis of the corpus striatum complex made by KAPPERS (cf. KAPPERS 1928, KAPPERS-HUBER-CROSBY 1936) has been of great importance. He based his studies chiefly on adult material, however, and lay the greatest stress on the fibre connexions of the different regions. He tried to arrange a phylogenetic series of different striata. In fishes a first, non-olfactory region is distinguished near the diencephalon, the palaeostriatum. In amphibians an archistriatum and a neostriatum are added, which in reptiles, birds and mammals are still more enlarged.

KIESEWALTER (1928) proposed a scheme of the tetrapod forebrain. In the subpallium (=Basis) he distinguished an olfacto-parolfactorium and a ventrolateral region. The latter includes the "lens", "amygdala" and "striatum". The "lens" corresponds roughly to CROSBY's (1917) ventrolateral area in reptiles, the "amygdala" to her intermediolateral area, and the "striatum" to the dorsolateral area. In mammals the "lens" contains the globus pallidus and the "striatum" the nucleus caudatus and the putamen. No ontogenetic investigations underlay KIESEWALTER's classification.

KUHLENBECK described in a series of papers the vertebrate forebrain, especially the amphibian and the reptilian forebrains, and summarized his idea of the homologies between the nuclei in a number of "Bauformeln" (1929 a). He then used the ventricular furrows as marks, after which the homologies were settled. His studies were chiefly carried out on adult material.

JOHNSTON has studied a great number of vertebrate forebrains in some papers and also tried to compare the different types with one another (1923 a and b). In selachians in principle the following subpallial regions are distinguished: a medial olfactory area, a basal area, a lateral olfactory area, a deep gray mass situated ventricular to the latter, and a somatic area. The medial olfactory area gives rise to the medial parolfactory nucleus (=the nucleus medialis septi) in reptiles and probably to the anterior olfactory nucleus. The basal area contains the anlage of the tuberculum olfactorium, the nucleus of the diagonal band and the anterior perforate space. The lateral olfactory area develops into the nucleus olfactorius

lateralis and the lobus pyriformis. The deep gray ventricular to the lateral olfactory area forms the caput nuclei caudati and the bed of the stria terminalis. The somatic area develops into the nucleus lentiformis. JOHNSTON was of the opinion that the only striatal component present in mammals but not present in selachians is the nucleus caudatus. It is formed in reptiles as the dorsal ventricular ridge. Possibly it is indicated in dipnoans. — JOHNSTON worked chiefly on adult material and laid great emphasis on the relation between the nuclei and the furrows. Some ontogenetical studies were, nevertheless, also carried out, as mentioned above.

HOLMGREN has in a series of papers described the vertebrate forebrain and proposed homologies on a chiefly embryological basis. His followers SÖDERBERG (1922), BÄCKSTRÖM (1924) and RUDEBECK (1945) have further supplemented these observations. In 1922 HOLMGREN assembled the results obtained from studies on the telencephalon of lower vertebrates (cyclostomes, selachians, actinopterygians, dipnoans) and suggested one scheme for the inverted brain type and one for the everted brain type. The homologies between these two types were also investigated. SÖDERBERG added urodeles and anurans to this scheme. In 1925 HOLMGREN described the ontogenesis in reptiles and mammals and compared these brains with those of lower vertebrates. BÄCKSTRÖM (elasmobranchs) and RUDEBECK (dipnoans) supplemented these observations but mainly agreed with HOLMGREN's apprehension of the homologies.

In *Petromyzon* HOLMGREN did not describe any subdivisions in the subpallium. In the other anamnians the following regions were distinguished: the nucleus olfactorius lateralis (sometimes divided into a pars dorsalis and a pars ventralis), the tuberculum olfactorium, the nucleus lateralis septi, the nucleus medialis septi, the nucleus taeniae, the nucleus dorsalis striatici and the nucleus ventralis striatici. HOLMGREN was of the opinion that the nucleus taeniae developed from the caudal part of the tuberculum olfactorium, but, as pointed out above, it has been shown that this is not the case in actinopterygians.

In amniotes HOLMGREN also described a lateral and a medial septal nucleus and some striatal nuclei. He maintained that the striatal complex is built up by three cellular columns, each consisting of three layers. They have previously (IV) been reviewed by the author. The dorsalmost column corresponds to the dorsal parts of the nucleus dorsalis striatici and the nucleus olfactorius lateralis; the middle column to the ventral parts of the same nuclei; the ventral column to the nucleus ventralis striatici and the tuberculum olfactorium.

Among all these authors only HOLMGREN and his co-workers have built the homologies on an exclusively ontogenetic basis. As has been pointed out previously by the author (especially in IV, VI and VII) some mistakes have probably been made by these authors when studying the ontogenesis. Our knowledge of the ontogenetic development, e. g., in actinopterygians, has also been incomplete, and the author has endeavoured to make a contribution to this subject with his studies. A comparison of the subpallial structures of different vertebrates will be made from the results obtained in this way. As the only basis of homologization the

cellular formations themselves will be used. In accordance with the principles put forward above, the relations between the nuclear masses and the ventricular sulci will not be taken into consideration.

b. *The author's results*

1. The subpallial cell columns

In the subpallial migration area (= the area ventralis telencephali) there is rostrally a subdivision into two or three columns in early stages. Caudally they fuse and form a united mass. The latter corresponds topographically to the preoptic recess in broad outlines and is thus rostrally limited by the commissure bed. This undifferentiated cell mass is the regio preoptica. As has been pointed out in the foregoing (chapter 6), the pallial migration area also enters this part in a few species.

In *Petromyzon* there is rostrally a division into two parts, a pars dorsalis and a pars ventralis (VII). Within the latter HEIER's (1948) nucleus medialis septi, nucleus lateralis septi and nucleus commissurae supraopticae develop, while the former gives rise to the corpus striatum of HEIER.

In elasmobranchs (VII), the rostral lobes of bony ganoids (I), urodeles (VII), anurans (VII), dipnoans (RUDEBECK), reptiles (IV) and mammals (VI) there is an early division into three cell columns in the rostral part of the area ventralis telencephali (= the subpallium). Very often they do not develop simultaneously but the dorsal or the ventral one forms first. There is, however, never any long interval between their appearances. In all cases the dorsal column and the ventral column are made up of relatively narrow bands, and the middle column holds a larger part of the ventricular gray. According to the author's opinion it is quite certain that these columns are homologous in different species.

In teleosts (I, III) only two parts develop in the area ventralis, a narrow dorsal and a larger ventral column. Not until relatively late is the latter one divided into two parts: a smaller one furthest ventrally and a larger one, situated between the dorsal and the ventralmost parts. The same conditions are present in the unevaginated part of the telencephalon of ganoids and bony ganoids (I, III). In this way the homologies between the columns in these brains and those of the brains with three columns can be settled, because in the rostral part of the forebrain of bony ganoids there are three columns present in embryonal stages. The dorsalmost column in the unevaginated part of the brain has been shown (I) to continue directly into the dorsalmost column in the evaginated part [= the nucleus olfactorius lateralis (I)]. So the ventral part of the area ventralis in the unevaginated actinopterygian forebrain corresponds to the two ventralmost columns in the forebrains with three columns.

Owing to these facts it seems likely that the ventral part of the area ventralis in *Petromyzon* also corresponds to the two ventralmost cell columns in the brains with three columns.

2. The dorsalmost subpallial column

In mammals it has been shown (VI) that the dorsalmost subpallial column (then called *c*) gives rise to the following nuclei: the nucleus of the lateral olfactory tract, the nucleus corticalis amygdalae, the globus pallidus, the nucleus centralis amygdalae with the anterior amygdaloid mass, the nucleus caudatus and the putamen. The detailed development of these nuclei occurs in the following manner: the cells migrate in two successive periods and thus form an external (c^I) and an internal (c^{II}) migrated layer or proliferation layer. Within the former there is a division into an external part (c_{ext}^I) and an internal part (c_{int}^I). c_{ext}^I develops into the nucleus of the lateral olfactory tract (rostrally) and the nucleus corticalis amygdalae (caudally). c_{int}^I forms the globus pallidus and its derivative, the nucleus basalis (rostrally), and the nucleus centralis amygdalae and its derivative, the anterior amygdaloid mass (caudally). Also within c^{II} a division occurs into an external part — the putamen — and an internal part — the nucleus caudatus.

Part of *c* enters the septum in mammals, brought there by the rostral evagination. The septal nuclei will, however, be discussed below.

The conditions in reptiles have been studied in detail (IV) and the homologies between the nuclei there and in mammals have been discussed (VI).

The avian forebrain has not yet been studied by the author. From earlier authors (DURWARD 1934 et al.) we know that the avian forebrain very greatly resembles that of reptiles. For this reason the avian telencephalon was thought to be of less importance for the discussion carried out here.³

In dipnoans (RUDEBECK) there is in this part a continual proliferation, forming the nucleus olfactorius lateralis, which can be divided into a dorsal and a ventral part.

Similar conditions are present in urodeles (VII).

In anurans, however, two successive proliferations occur in this region, even if the second one is rather faint. A peripheral nucleus (SÖDERBERG's nucleus olfactorius lateralis) and a ventricular nucleus (SÖDERBERG's nucleus dorsalis striatici) thus develop. If the abbreviations used in amniotes are applied to them, they represent a c^I and a c^{II} respectively.

Also in elasmobranchs a c^I and a c^{II} develop (the nucleus olfactorius lateralis and the nucleus dorsalis striatici BÄCKSTRÖM). In anurans as well as in elasmobranchs they fuse secondarily.

In the unevaginated part of the actinopterygian forebrain a continual migration takes place and the nucleus olfactorius lateralis (*I*; *n.*? in KÄLLÉN 1947) develops.

³ Another vertebrate class not investigated here is myxinoidei. On account of the complete lack of embryos of such vertebrates, the author was not able to study that type of brain. The structure of the adult brain is well-known by HOLMGREN's (1919) and JANSEN's (1930) works, but little is known of their embryology. CONEL (1931) described the external and ventricular contours of some *Bdellostoma* stages, but his material did not permit any observations on the nuclei. HOLMGREN (1946) gave a few notes on a *Myxine* embryo, but also his specimen was ill preserved.

In the evaginated part two layers are formed in the embryo, an external [the nucleus olfactorius lateralis (*II*)] and a ventricular. They fuse again later on.

In *Petromyzon* only the ventricular corpus striatum (HEIER) develops.

According to these results the nucleus olfactorius lateralis of lower vertebrates is the homology of the following mammalian nuclei: the nucleus of the lateral olfactory tract, the nucleus corticalis amygdalae, the globus pallidus, the nucleus basalis, the nucleus centralis amygdalae and the anterior amygdaloid mass. The nucleus dorsalis striatici is the homology of the nucleus caudatus and the putamen.

In anurans and elasmobranchs a nucleus dorsalis striatici is developed during the ontogenesis, but in the adult animal it is fused with the nucleus olfactorius lateralis. As a fitting name for this complex formation the author suggests formatio subpallialis lateralis.

3. The middle subpallial column

In mammals there are (*VI*) in this column (*b*) two successive proliferations, forming b^I and b^{II} . The former represents the tuberculum olfactorium, the latter the nucleus accumbens, the caput nuclei caudati and the bed of the stria terminalis.

Also in reptiles (*IV*) a b^I , the tuberculum olfactorium, and a b^{II} , the nucleus accumbens, develop.

In dipnoans (RUDEBECK) a migrated layer develops caudally in this region (the tuberculum olfactorium cortex RUDEBECK), while rostrally the ventricular and the migrated parts are united.

In urodeles (*VII*) a migrated cell layer is never formed, but the cell column *b* lies ventricularly.

In anurans (SÖDERBERG) a b^I and a b^{II} develops during the ontogenesis. They fuse, however, later on, except in the caudalmost part, where b^I remains as the nucleus taeniae, while b^{II} forms the tail of the caudate (SÖDERBERG).

In elasmobranchs (HOLMGREN et al.) a b^I and a b^{II} also develop. The former gives rise to the adult tuberculum olfactorium, the nucleus taeniae and the "somatic area", while the latter forms the nucleus ventralis striatici (BÄCKSTRÖM).

In bony ganoids a peripheral layer and a ventricular layer develop in the rostral lobe, but in the unevaginated part of the forebrain they are connected. This is also the case in the brains of other actinopterygians. As pointed out before, it is not possible in young stages to distinguish between the two ventralmost cell columns in this part of the brain. Later on the cell mass, however, is divided into a dorsal part, the corpus precommissurale pars superior, and a ventral part, the corpus precommissurale pars inferior. The pars superior has been supposed to correspond roughly to *b*.

In *Petromyzon* a condensation of the cells occurs in the two fused ventral columns. This condensation is the nucleus commissurae supraopticae (HEIER). The rest (the nucleus olfactorius medialis JOHNSTON) is divided into a nucleus medialis septi and a nucleus lateralis septi (HEIER). Together they correspond to the cell column *b* and the cell column *a* (e. g. the ventralmost subpallial column).

The three peripheral cell structures in *b* in elasmobranchs: the tuberculum olfactorium, the nucleus taeniae and the "somatic area", thus correspond together to the tuberculum olfactorium in amniotes. A better name for the rostralmost formation — the tuberculum olfactorium (HOLMGREN, BÄCKSTRÖM) — is, therefore, the nucleus superficialis basalis in analogy with area superficialis basalis, a name used by JOHNSTON et al. The cell mass situated ventricular hereto represents the anlage of the nucleus accumbens, the caput nuclei caudati and the bed of the stria terminalis in mammals. As a neutral name for this formation, the nucleus ventralis striatici, proposed by BÄCKSTRÖM, may be used.

The cell column *b* in urodeles, actinopterygians, dipnoans and *Petromyzon* represents the tuberculum olfactorium as only one proliferation takes place. In anurans two successive proliferations take place, but the two nuclei formed in this way fuse except rostrally. The fused masses may be called the formatio subpallialis ventralis. The ventricular, caudal cell mass, which remains free in the adult (the cauda nuclei caudati SÖDERBERG), corresponds to the caudal part of the reptilian nucleus accumbens and roughly to the mammalian bed of the stria terminalis.

In addition to the derivatives from *b* now described, a septal component is present in amniotes, which will be described more in detail below. There is also a component from this cell column present in the amygdaloid complex. It seems to be impossible to detect any homology between the latter and any nucleus in lower vertebrates.

4. The septal nuclei

In amniotes (*IV*, *V*, *VI*) the septal nuclei are formed from all three cell columns. By the rostral true evagination, *c* is dislocated into the septum and builds up the rostral part, while the ventral evagination brings part of *b* and the whole of *a* (=the ventralmost cell column) into the septum. From *a* the nucleus medialis septi and the nucleus of the diagonal band develops, possibly also the nucleus dorsalis septi (=the nucleus septo-hippocampalis), all of them by a continual proliferation process. The septal part of *c* (c_m) forms the area parolfactoria (JOHNSTON) in reptiles, while the septal part of *b* (b_m) forms the nucleus lateralis septi. In mammals c_m and b_m fuse and give rise to the nucleus lateralis septi.

In anurans the author has shown (*VII*) that the septal nuclei develop from two places. The nucleus lateralis septi (SÖDERBERG et al.) develops from the cell column *c*, which is brought into the septum by the rostral true evagination. It thus represents c_m . The nucleus medialis septi (SÖDERBERG et al.), however, grows out from the ventral cell column (*a*) developing rostralwards and lies peripheral to the nucleus lateralis septi. It thus represents the amniote nucleus medialis septi, nucleus of the diagonal band and possibly nucleus dorsalis septi.

In urodeles the dorsal cell column also enters the septum and forms the so-called eminentia postolfactoria. The rest of the septum formation is built up by the cell column *a*, within which a secondary subdivision into a superficial and a deep part is visible (*VII*).

In bony ganoids a nucleus can be distinguished in the rostral lobe, described under the name of the nucleus medialis septi (*I*). As is clearly visible in figures 2 and 9 in this paper (*I*), the cell mass in question extends from the ventralmost part of the wall. From here it reaches rostralwards and lies external to the ventricular layer. It forms here the ventralmost column (*a*) and its homology with the nucleus medialis septi in anurans and the corresponding complex in amniotes seems to be established. In bony ganoids a cell process grows caudalwards from the cell plug and lies lateral to the nucleus olfactorius lateralis (*I*). It enters the nuclear complex, called the nucleus olfactorius lateralis by HOLMGREN, JOHNSTON et al. The author has found no correspondence to this cell process in inverted brains except in dipnoans (see below). It might be included — as was done in the paper *I* — in the nucleus medialis septi.

In the unevaginated part of the telencephalon of bony ganoids there occurs, as mentioned above, a division of the cell mass situated ventral to *c*, into a dorsal and a ventral part. It is not possible, however, to follow the ventral part to *a* in the rostral lobe or the dorsal part to *b*. For this reason the homologies between these regions cannot be determined exactly. Above a rough homology has been supposed between the dorsal part (the corpus precommissurale pars superior) and *b*. Thus the ventral part (the corpus precommissurale pars inferior) would roughly correspond to *a*.

In teleosts a similar division occurs in the ventricularly situated cells, and the same homologies can be assumed. Moreover, a cell mass grows peripherally caudalwards from the caudal part of the granular layer of the olfactory bulb. This mass is thus formed similarly to the cell process described above in bony ganoids and a homology between these structures has previously been supposed (*I*). They ought to be included in the medial septal nucleus-complex together with the corpus precommissurale pars inferior.

It has been shown (*VII*) that in elasmobranchs the septal nuclei consist of three structures. Rostralmost lies a cell mass, which rostrally continues into the nucleus olfactorius lateralis and represents c_m . On a level with the thickened lamina terminalis lies another cell mass, which represents the ventralmost cell column, *a*. In later stages a new cell mass is formed ventricular to the latter by a second proliferation. Thus this illustrates that two successive proliferations can take place in the cell column *a*, too: one a^I , which forms the caudal part of the nucleus medialis septi of HOLMGREN et al., and one a^{II} , which forms the nucleus lateralis septi of the same authors. a^I represents the correspondence of the nucleus medialis septi in, e. g., anurans.

The septal nuclei in dipnoans have been carefully studied by RUDEBECK, and the author (*VII*) has somewhat supplemented and discussed his observations. RUDEBECK distinguished a pars dorsalis and a pars ventralis septi. Within the former a ventricular cell mass and a peripheral one are present. The ventricular one [HOLMGREN-VAN DER HORST's (1925) nucleus intermedius septi, RUDEBECK's nucleus lateralis septi] represents a c_m , while the peripheral one grows out (according to

RUDEBECK) from the caudal part of the granular layer of the olfactory bulb. This nucleus (HOLMGREN-VAN DER HORST's nucleus lateralis septi, RUDEBECK's nucleus medialis septi p. dorsalis) can thus be roughly compared with the peripheral cell process in the actinopterygian forebrain (see above). The pars ventralis septi is built up by the part of the septum formed by the ventral evagination. In it lies a ventricular layer, which is formed by the medialmost part of the middle column (*b*) and thus corresponds to b_m in amniotes. Peripheral to it lies HOLMGREN-VAN DER HORST's nucleus medialis septi (RUDEBECK's nucleus medialis septi p. ventralis), which develops from the ventralmost column (*a*) and thus represents the nucleus medialis septi in anurans i. a.

It seems to be clear that the septal region shows a very great variation, especially among lower vertebrates. A contributory reason to this is the variation in the formation of the hemisphere (cf. chapter 3). Apart from this there are great dissimilarities among the different species with regard to the septal nuclei.

5. The strio-amygdaloid complex

This name was originally used for a structure in the mammalian forebrain, especially in *Homo*. The following nuclei were included: the nucleus caudatus with the caput nuclei caudati, the nucleus lentiformis, built up by the putamen and the globus pallidus, the bed of the stria terminalis, the claustrum and the "nucleus amygdalae" or the amygdaloid complex, formed chiefly by the following nuclei: the nucleus lateralis, basalis, medialis, centralis and corticalis amygdalae and the anterior amygdaloid mass.

Attempts to settle the homologies of these nuclei in lower vertebrates have been made for a long time, as is apparent from the survey of the literature given above.

If the nuclei in question are looked upon as purely morphological conceptions, only ontogenetical investigations can show their homologies in lower animals, as pointed out above. Then the difficulties arise due to the fact that the strio-amygdaloid complex does not appear to be an ontogenetic unity. As shown previously (HOLMGREN 1925 and the author VI) the mammalian amygdaloid complex is derived from the pallium (the nucleus lateralis and basalis) as well as from the subpallium (the rest of the amygdaloid nuclei). — MACCHI (1949), on the contrary, was of the opinion that the whole of the amygdaloid complex in *Homo* was of subpallial origin. — The claustrum is a pallial component, developed in connexion with the pallial amygdaloid nuclei. The nucleus caudatus and the nucleus lentiformis are subpallial derivatives. Among the subpallial components in the strio-amygdaloid complex, most nuclei develop from the cell column *c*, but some — the caput nuclei caudati, the bed of the stria terminalis and the nucleus accumbens, if it is included in the strio-amygdaloid complex, together with the medial amygdaloid nucleus. — develop from the cell column *b*.

In reptiles most components of the strio-amygdaloid complex have been identified (VI), so in this case one can justifiably talk about such a complex.

TABLE 1.
Comparison between the subpallial nuclei in *Amniota* and *Anamnia*.

Petromyzon (HEIER 1948)	Elasmobranchii (BÄCKSTRÖM 1924)	Actinopterygii (KÄLLÉN 1947)	Urodela (SÖDERBERG 1922)	Anura (SÖDERBERG 1922)	Dipnoi (RUDEBECK 1945)	Amniota (KÄLLÉN VI)
c.s.	nc. olf. lat.	nc. olf. lat.	part of tub. olf. + nc. taen.	nc. olf. lat.	nc. olf. lat.	$c_{ert}^I + c_{int}^I$
— — —	nc. d. str.	— — —	— — —	nc. d. str.	— — —	c^{II}
part of nc. olf. med.	som. a.	tub. olf.	part of tub. olf. + nc. taen.	tub. olf. + nc. taen.	tub. olf. + nc. taen.	b^I
	tub. olf. + nc. taen.					
— — —	nc. v. str.	— — —	— — —	nc. v. str.	— — —	b^{II}
— — —	nc. med. septi p. rostr.	— — —	em. postolf.	nc. lat. septi	nc. lat. septi	c_m
— — —	— — —	nc. med. septi	— — —	— — —	nc. med. septi p. dors.	— — —
part of nc. olf. med.	nc. med. septi p. caud.	nc. lat. septi	nc. med. septi + nc. lat. septi	nc. med. septi	nc. med. septi p. ventr.	$a + a_{ert}$
— — —	nc. lat. septi	— — —	— — —	— — —	— — —	— — —
lob. s.h.	— — —	nc. taen.	mass. cell. reun.	mass. cell. reun.	nc. preopt. p. sup.	— — —

Only the claustral anlage (= the claustrum and the pallial amygdaloid nuclei) is lacking, but instead a dorsal ventricular ridge (= the hypopallium) is developed — also from the pallium.

In lower vertebrates there is no correspondence to the reptilian dorsal ventricular ridge or the mammalian claustral anlage. No pallial part of the strio-amygdaloid complex is thus developed.

The mammalian medial amygdaloid nucleus and the reptilian nuclei ventromedialis and interstitialis have not been identified in lower vertebrates. The *b^{II}*-formation — the mammalian nucleus accumbens, caput nuclei caudati and the bed of the stria terminalis — is present in some lower vertebrates as a transitory formation, but remains in the adult animal only in anurans. As pointed out above this nucleus (cauda nuclei caudati SÖDERBERG) can be compared with the mammalian bed of the stria terminalis, because it represents the caudalmost part of the *b^{II}*-formation.

The rest of the strio-amygdaloid complex develops from the cell column *c*. This has been described in all vertebrates and is differentiated into two parts (*c^I* and *c^{II}*) during embryonal stages of some of them.

In lower vertebrates the strio-amygdaloid complex is thus only represented by the very slightly differentiated cell column *c* (the nucleus olfactorius lateralis or the formatio subpallialis lateralis) and in some species by a nucleus ventralis striatici (*b^{II}*).

The most important of the homologies between the nuclei, studied in chapter 9, are summarized in table 1. The abbreviations used in this table, some of which have also been used in the figures in this paper, are collected and translated after the text. No distinction has been made between the brains of mammals and reptiles. The homologies between the nuclei in these brains are tabulated in table 5 in paper VI.

The nomenclature used refers to the authors mentioned within brackets at the head of the table after the name of the species. In some cases smaller changes have been made.

X. Summary

1. The only basis for the homologization of brain nuclei ought to be the ontogenetic development of the nuclei from the regions, where the first morphologically visible cell migration takes place, the so-called migration areas [roughly corresponding to BERGQUIST's (1932) "Grundgebieten"].

2. The ventricular furrows seem to be related to the proliferation processes of the brain, but are of less importance for the study of the cell migration and the homologization of the nuclei.

3. In all vertebrates studied two migration areas are formed in the telencephalon: the area dorsalis telencephali and the area ventralis telencephali. The former gives rise to the pallium, the latter to the subpallium.

4. In most vertebrates the area dorsalis telencephali continues caudally into the area frontalis thalami in young stages, while the area ventralis telencephali and the area preoptica are united. In elasmobranchs and in young *Ambystoma* stages the area dorsalis telencephali and the area frontalis thalami are separated. In these species both the area dorsalis telencephali and the area ventralis telencephali enter the formation of the area preoptica.

5. It does not seem to be possible to determine any morphological di-telencephalic boundary.

6. No shifting in a proper sense of the olfactory nerve takes place. Usually the nerve enters at the boundary between the area dorsalis and the area ventralis telencephali. Around the entrance of the nerve an area bulbaris develops, which contains the anlage of the olfactory bulb and the structures related to it.

7. With the results on the ontogenesis of the nuclei obtained in earlier papers, as a basis, homologies between some structures in the vertebrate telencephalon are proposed, especially in the subpallium. The most important results are summarized in table 1.

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XIII. Abbreviations

$a+a_{ext}$	the ventralmost column in amniotes
<i>a.c.th.</i>	area caudalis thalami
<i>a.d.</i>	area dorsalis telencephali
<i>a.fr.th.</i>	area frontalis thalami
<i>a.m.th.</i>	area medialis thalami
<i>a.preopt.</i>	area preoptica
<i>a.v.</i>	area ventralis telencephali
<i>bl</i>	the first proliferation layer in the middle subpallial column in amniotes
<i>blI</i>	the second proliferation layer in the same
$c_{ext}^I + c_{int}^I$	the first proliferation layer in the dorsalmost subpallial column in amniotes
<i>clI</i>	the second proliferation layer in the same
<i>c_m</i>	the septal part of the same column
<i>c.s.</i>	corpus striatum in <i>Petromyzon</i>
<i>em.postolf.</i>	eminentia postolfactoria
<i>lob.s-h.</i>	lobus subhippocampalis
<i>mass.cell.reun.</i>	massa cellularis reueniens
<i>nc.d.str.</i>	nucleus dorsalis striatici
<i>nc.lat.septi</i>	nucleus lateralis septi
<i>nc.med.septi</i>	nucleus medialis septi
<i>nc.med.septi p.caud.</i>	caudal part of the nucleus medialis septi
<i>nc.med.septi p.dors.</i>	dorsal " " " " " "
<i>nc.med.septi p.rostr.</i>	rostral " " " " " "
<i>nc.med.septi p.ventr.</i>	ventral " " " " " "
<i>nc.olf.lat.</i>	nucleus olfactorius lateralis
<i>nc.olf.med.</i>	nucleus olfactorius medialis
<i>nc.preopt.p.sup.</i>	nucleus preopticus pars superior
<i>nc.taen.</i>	nucleus taeniae
<i>nc.v.str.</i>	nucleus ventralis striatici
<i>som.a.</i>	somatic area JOHNSTON
<i>tub.olf.</i>	tuberculum olfactorium

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